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Rita A. Horner; David L. Garrison; F. Gerald Plumley

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Harmful algal blooms and red tide problems on the U.S. west coast

Rita A. Horner[1]
School of Oceanography, Box 357940, University of Washington, Seattle, Washington 98195-7940

David L. Garrison
Institute of Marine Sciences, University of California, Santa Cruz, California 95064

F. Gerald Plumley
Institute of Marine Science, University of Alaska, Fairbanks, Alaska 99709

Abstract

On the U.S. west coast, the main toxin-producing algal species are dinoflagellates in the genus *Alexandrium* that cause paralytic shellfish poisoning (PSP) and diatoms in the genus *Pseudo-nitzschia* that produce domoic acid and cause domoic acid poisoning (DAP). Other harmful species, including the raphidophyte *Heterosigma akashiwo* and the diatoms *Chaetoceros convolutus* and *Chaetoceros concavicornis,* kill fish at aquaculture sites, but are not harmful to humans. Water discolorations (red tides) caused by nontoxic dinoflagellates also occur throughout the area. Early records, partially based on local native lore, suggest that algal toxins have been present along this coast for hundreds of years, but actual scientific information is sparse. We review what is now known about harmful algal blooms in this vast area, including the hydrographic regimes that induce and(or) support blooms, bloom dynamics, and the biology of the causative species.

The increase in toxic, noxious, or otherwise harmful algal blooms (HABs) that is apparently occurring world-wide (e.g. Smayda 1990; Anderson 1995) has also been seen on the west coast of North America (e.g. Garrison et al. 1992; Horner and Postel 1993; Taylor and Horner 1994; Walz et al. 1994). Only about two dozen of the more than 5,000 known phytoplankton species produce toxins or directly cause fish mortalities, while another 20–30 species are responsible for other problems, such as water discolorations, along the west coast (Table 1). Paralytic shellfish poisoning (PSP), resulting from a number of saxitoxin derivatives produced by dinoflagellates in the genus *Alexandrium,* and domoic acid poisoning (DAP; also called amnesic shellfish poisoning, ASP), caused by diatoms in the genus *Pseudo-nitzschia,* are the primary harmful algal bloom problems on the west coast. Other toxic species, e.g. *Dinophysis* spp. associated with diarrhetic shellfish poisoning (DSP) in Japan and northern Europe, are present in the area, but DSP has not yet been reported. In Washington State, with a large aquaculture industry raising salmonids in net pens, the raphidophyte flagellate *Heterosigma akashiwo* and the diatoms *Chaetoceros concavicornis, Chaetoceros convolutus,* and perhaps *Chaetoceros danicus* sometimes cause extensive fish kills. In Alaska, bitter crab disease, caused by a parasitic dinoflagellate, kills Tanner crabs. Although this latter infection is not a typical harmful algal "bloom," extensive crab mortalities occur and the food web is affected. In addition, red tides produced when dinoflagellates are abundant enough to discolor the surface waters occur throughout the west coast region. None of the red tide-forming species are known to be toxic. However, dense blooms may kill shellfish and other invertebrates due to low oxygen levels as the blooms decay and may also influence the behavior and feeding of zooplankton, altering food-web dynamics.

In this report, we review pertinent information about the harmful algae, how major hydrographic regimes along the coast induce and(or) nourish blooms of these species, and highlight major questions that should be addressed in order to understand their biology and bloom dynamics. A brief survey of the large-scale hydrography of the Pacific coast provides the context for understanding algal bloom dynamics over this large region. It must be pointed out that there are few long-term records for phytoplankton cycles from the area, so much of the present information comes from measurements of toxins in shellfish rather than from knowledge of the toxic phytoplankton species and bloom dynamics.

The environmental setting

The physical and chemical characteristics of Pacific coastal waters are structured by large-scale ocean circulation patterns. The North Pacific Current, or West Wind Drift, approaches the west coast at ~45°N (Fig. 1), where a small part of the flow turns north along the coast of northern Washington, British Columbia, and Alaska as part of the Alaskan Gyre System, and the larger portion turns southward to form the California Current System (Reid et al. 1958).

The northern branch of the eastward-flowing North Pacific Current becomes the Alaska Current, forming a broad band (300 km wide) of moderately slow-moving water (20–30 cm s^{-1}) that generally follows the continental slope northward

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[1] Corresponding author.

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Table 1. Toxic and nontoxic algal species reported from the west coast of North America. The nomenclature of some taxa has undergone revision recently so synonymies (in parentheses) are included.

1. Dinoflagellate species which produce saxitoxins that cause paralytic shellfish poisoning (PSP).
   - *Alexandrium acatenella* (Whedon & Kofoid) Balech
   - *Alexandrium catenella* (Whedon & Kofoid) Balech
   - *Alexandrium fundyense* Balech
   - *Alexandrium hiranoi* Kita & Fukuyo
   - *Alexandrium ostenfeldii* (Paulsen) Balech & Tangen
   - *Alexandrium tamarense* (Lebour) Balech
     - (Synonmyms for *Alexandrium* Halim have been *Gonyaulax* Diesing, *Gesnerium* Halim, and *Protogonyaulax* Taylor).
2. Dinoflagellate species which produce okadaic acid that causes diarrhetic shellfish poisoning (DSP). DSP is not currently known from the west coast, but the causative organisms are common.
   - *Dinophysis acuminata* Claparède & Lachmann
   - *Dinophysis acuta* Ehrenberg
   - *Dinophysis fortii* Pavillard
   - *Dinophysis norvegica* Claparède & Lachmann
3. Planktonic diatoms which produce domoic acid that causes domoic acid poisoning (DAP; also known as amnesic shellfish poisoning [ASP]).
   - *Pseudo-nitzschia australis* Frenguelli (*Nitzschia pseudoseriata* Hasle)
   - *Pseudo-nitzschia multiseries* (Hasle) Hasle (*Nitzschia pungens* f. *multiseries* Hasle, *Pseudonitzschia pungens* f. *multiseries* (Hasle) Hasle)
   - *Pseudo-nitzschia pseudodelicatissima* (Hasle) Hasle (*Nitzschia delicatula* Hasle; *Nitzschia pseudodelicatissima* Hasle)
   - *Pseudo-nitzschia pungens* (Grunow in Cleve and Möller) Hasle (*Nitzschia pungens* Grunow)
   - *Pseudo-nitzschia seriata* (P.T. Cleve) H. Peragallo (*Nitzschia seriata* P.T. Cleve)
     - These species were originally members of the section *Pseudonitzschia* in the genus *Nitzschia,* but are now recognized as the genus *Pseudo-nitzschia* (Hasle 1993).
4. Species associated with fish kills, but not known to be harmful to humans.
   - Diatoms
     - *Chaetoceros concavicornis* Mangin
     - *Chaetoceros convolutus* Castracane
     - *Chaetoceros danicus* Cleve
   - Raphidophyte
     - *Heterosigma akashiwo* (Hada) Hada *ex* Sournia (*Olisthodiscus carterae* Hulburt, *Heterosigma carterae* (Hulburt) Taylor; often confused with *Olisthodiscus luteus* Carter)
5. Species that cause water discolorations (i.e. "red tides"). Blooms of these species may kill fish or invertebrates due to oxygen depletion, may change or disrupt food-web dynamics, or produce noxious compounds (e.g. *Phaeocystis*).
   - Dinoflagellates
     - *Ceratium dens* Ostenfeld & Schmidt
     - *Ceratium divaricatum* Lemmermann
     - *Ceratium furca* (Ehrenberg) Claparède & Lachmann
     - *Ceratium fusus* (Ehrenberg) Dujardin
     - *Ceratium* spp.
     - *Gymnodinium sanguineum* Hirasaka (*Gymnodinium splendens* Lebour)
     - *Gymnodinium flavum* Kofoid & Swezy
     - *Lingulodinium polyedrum* (Stein) Dodge (*Gonyaulax polyedra* Stein)
     - *Noctiluca scintillans* (Macartney) Kofoid & Swezy (*Noctiluca miliaris* Suriray; *Medusa scintillans* Macartney)
     - *Prorocentrum micans* Ehrenberg
     - *Protoperidinium* Bergh (*Peridinium* Ehrenberg)
   - Diatoms
     - *Rhizosolenia setigera* Brightwell
   - Prymnesiophyte flagellate
     - *Phaeocystis* Lagerheim
   - Ciliates
     - *Mesodinium rubrum* (Lohmann) Hamburger & Buddenbrock (*Myrionecta rubra* Grain et al. 1982; *Cyclotrichium meuneri* Powers).
6. Parasitic dinoflagellates.
   - *Hematodinium* Chatton et Poisson

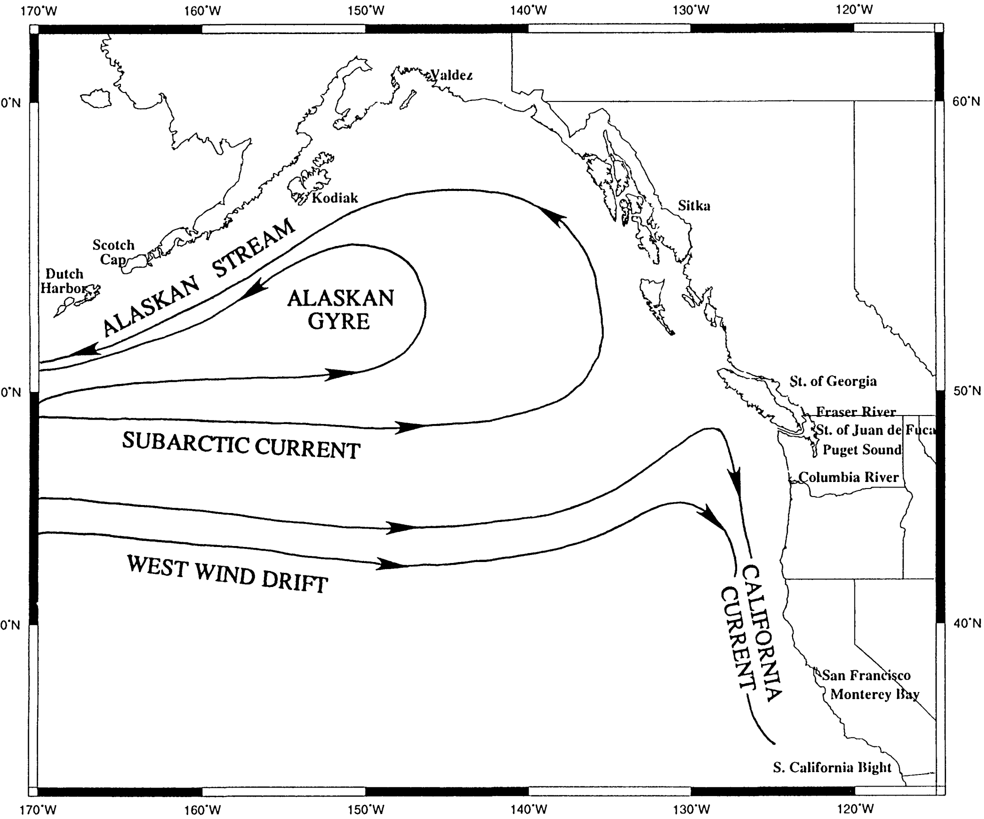

Fig. 1. Schematic representation of the major currents on the U.S. Pacific Coast. (Adapted from Dodimead et al. 1963.)

from Canada along southeastern Alaska. After turning westward, it becomes the Alaska Stream, a narrower (100 km wide) and faster (up to 100 cm s^{-1}) current, as it approaches the Aleutian Islands (Reed and Schumacher 1986). The nearshore Alaska Coastal Current, with a seaward boundary approximately at the edge of the continental shelf, follows a similar path, but it is faster, more variable, and is greatly affected by local shoreline topography. The water mass characteristics of the coastal current are markedly influenced by freshwater input from fjords and estuaries (Royer 1979, 1981; Schumacher and Reed 1980). Precipitation is high, ranging between 40 and 800 cm yr^{-1} in southeast Alaska and providing annual-mean-runoff rates of 23×10^3 m^3 s^{-1}. The runoff is confined by wind-induced Ekman transport to a narrow current jet close to shore (Wilson and Overland 1986). During winter, strong shoreward winds arising from the Aleutian Low cause considerable downwelling of nearshore waters; the replacement of the Aleutian Low with the North Pacific High in summer results in relaxation of downwelling, but likely permits intrusion of deep water onto the shelf. The mechanisms underlying vertical transport of this nutrient-rich bottom water into the euphotic zone are uncertain (T. Royer pers. comm.) but may include mesoscale eddies and steering by canyons and shoal regions. Baroclinic instabilities in the Alaska Coastal Current may induce vertical velocities of up to 20 m d^{-1} (Barth unpubl.). Regardless of the physical mechanism responsible for nutrient enrichment of the euphotic zone, the consequences are high rates of production and the development of large seasonal algal blooms.

The southerly flowing branch of the North Pacific Current becomes the California Current System (CCS). The largest component of the CCS is the broad ($\sim$1,000 km), shallow (<500 m deep), slow-moving (<25 cm s^{-1}) California Current which flows equatorward year-round and brings cold, low salinity, highly oxygenated, nutrient-rich subarctic water to lower latitudes (Reid et al. 1958; Lynn and Simpson 1987; Hickey 1989). Beneath the California Current and confined to the region of the continental slope (usually within 150 km of the coast), the California Undercurrent transports warmer, more saline, and less oxygenated water poleward. In fall and winter, the Davidson Current flows poleward well seaward of the slope, from $\sim$35°N to 50°N (Point Conception to Vancouver Island) (Hickey in press).

The CCS is an eastern boundary current affected by seasonal coastal upwelling during spring and summer in response to strong and persistent northwest winds. Timing of the upwelling maximum varies with latitude, occurring early in spring in southern California (Reid et al. 1958), in June off Washington, and throughout summer off northern California and Oregon (Landry et al. 1989). The primary effect of upwelling is to bring cold, nutrient-rich water, which supports rich phytoplankton blooms, into the surface layer.

There is considerable interannual variability in the CCS, with El Niño-Southern Oscillation cycles (ENSOs) producing the most apparent interannual signal. ENSOs occur every

3–7 yr and result in increased northward transport of surface water, deepening of the thermocline, and higher sea surface temperatures (U.S. GLOBEC 1994).

Meso- and large-scale features also occur over the area, for example, intensification of upwelling in conjunction with headlands (Reid et al. 1958; U.S. GLOBEC 1994), areas of reduced circulation downstream from upwelling centers (Graham et al. 1992), cross-shelf circulation associated with upwelling cells, and jets and eddies that either transport nearshore water offshore or bring offshore waters into the shallow coastal regions (Flegal et al. 1993). One of the sharpest hydrographical and biological boundaries in the region occurs at Pt. Conception because of the general counterclockwise circulation in the Southern California Bight (U.S. GLOBEC 1994).

Nutrients

Nutrient concentrations in Alaskan open-ocean waters are generally in excess of those needed for plant growth (McAllister et al. 1960) with the possible exception of iron (Martin and Fitzwater 1988). The nutrient concentrations are poorly documented in waters on the shoreward side of the Alaska Current where HAB problems occur. Overall, nutrient levels are strongly influenced by the extent of intrusion of deep waters and convergence, mixing, precipitation, runoff from land, and seasonal utilization of nutrients by phytoplankton (Goering et al. 1973; Sambrotto and Lorenzen 1986). Nitrate concentrations near the surface at one station in Resurrection Bay ranged from $>20\ \mu M$ in winter to $<1\ \mu M$ in September (Reeburgh and Kipphut 1986).

In the Pacific Northwest, surface nutrient concentrations are generally high everywhere during winter, but are higher near the coast in summer when phytoplankton blooms may occur. The Columbia and Fraser Rivers are sources of high nitrate ($>5\ \mu M$), phosphate ($>1\ \mu M$), and silicate ($>20\ \mu M$) in both winter and summer with silicate being most influenced by the river plumes. The spring phytoplankton bloom (April) drastically reduces nutrient levels, with nitrate being affected to a greater extent than phosphate and silicate. Summer upwelling reintroduces nutrients to the coastal system (Landry et al. 1989).

Surface nutrients along the central California coast are typically high during the upwelling season (nitrate + nitrite $>5\ \mu M$; silicate $>10\ \mu M$) with lower levels characterizing the Davidson Current period during fall and winter (Malone 1971; Garrison 1979). Nutrients can reach low concentrations after upwelling periods and even during the upwelling period in shallow waters where well-developed blooms may reduce nitrate and silicate to undetectable levels (e.g. Broenkow and Smethie 1978; Garrison et al. 1992). Surface waters in the Southern California Bight are generally lower in nutrient concentrations than the offshore and more northerly regions of the CCS, with nutrients depleted in the surface 5–40 m (Eppley et al. 1978) except during periods of strong upwelling.

Seasonal phytoplankton blooms

The seasonal cycle of phytoplankton can best be characterized in California because more taxonomic information is available than for other areas. In Monterey Bay, the annual bloom cycle is similar to that of many cold temperate regions, with a spring bloom of chain-forming diatoms (Malone 1971; Garrison 1979) which may be sustained through summer in upwelling regions. Phytoplankton assemblages show a regular successional pattern from diatom- to dinoflagellate-dominated during periods of stratification (*see* Garrison 1979; Schrader 1981). However, successional patterns may be interrupted by periods of episodic upwelling, which result in a return to diatom-dominated assemblages (Garrison 1979). Farther north, in estuarine areas of the Strait of Georgia, diatoms are present in spring and summer; dinoflagellates are most abundant in summer, but may be present also in spring and winter; and autotrophic flagellates are common in late summer or winter in some inlets (Harrison et al. 1983). Ship-based sampling and remote-sensing techniques suggest phytoplankton blooms are most highly developed in shallow regions of the continental shelf (e.g. Malone 1971; Garrison 1979; Perry et al. 1989; Strub et al. 1990).

Specific HAB problems

Paralytic shellfish poisoning (PSP)—The earliest documented case of PSP on the U.S. west coast was in 1793 when five members of Captain George Vancouver's crew became ill and one died after eating mussels collected in Poison Cove on the central British Columbia Coast (Quayle 1969). A second incident occurred in 1799 when about 100 Aleut hunters working for Alexander Baranof died after eating mussels harvested near Sitka, Alaska. Pacific coast Indians were aware of PSP and believed that shellfish toxicity was related to red tides and bioluminescence (Meyer et al. 1928). There were also cases of PSP among early European settlers in California (Meyer et al. 1928; Sommer and Meyer 1937). By 1927, California recognized that PSP posed a serious health threat and began a prevention program. Later, Sommer et al. (1937) discovered that a dinoflagellate now known as *Alexandrium catenella* was the causative organism. In 1942, the deaths of three people in Washington State after eating clams and mussels collected in the Strait of Juan de Fuca, led to a summer ban for the harvest of all bivalve molluscs from Dungeness Spit on the strait to the mouth of the Columbia River, but it was not until 1965 that a specific species, the dinoflagellate *A. catenella,* was directly linked to an illness or fatality in the Pacific Northwest (Prakash and Taylor 1966). In Alaska, where the annual, sustainable shellfish harvest has been estimated as ~22 million kilograms (including shell weight) (Nevé and Reichardt 1984), the presence of PSP has severely limited the development of a large shellfish industry. The problem has been to correlate the abundance of a causative organism (presumably *Alexandrium* spp.) with the timing, levels, and geographic distribution of toxin in the shellfish (Hall 1982). Increased testing of commercially harvested shellfish has allowed the industry to grow in recent years, but vast expanses of coastline remain unexploited.

In all of the western states, most information on PSP-producing toxin episodes has been gathered from state monitoring programs (e.g. Nishitani and Chew 1988; Price et al.

1991; R. Barrett pers. comm.) and is thus based on detection of toxin in shellfish rather than on monitoring phytoplankton species composition and abundance. *A. catenella* is apparently the primary PSP producer in open coastal environments (Nishitani and Chew 1988; Price et al. 1991), but this has not been confirmed by adequate sampling and at least five other *Alexandrium* species are known from west coast waters (Table 1; Gaines and Taylor 1985; Scholin et al. 1994; Taylor and Horner 1994).

PSP-producing blooms are common on the California coast. From 1962 to 1989, there were toxic events in 22 of the 28 yr, with two or more events reported for 10 of them (Price et al. 1991). In all western states, isolated regional blooms occur in some years, while in others, incidences are widespread with high levels of toxin at several locations at the same time. Toxin is usually highest in July and August and most toxic events occur between May and October.

Observations in California, Oregon, Washington, and possibly Alaska suggest that blooms along the open coast are advected into estuaries and embayments from adjacent coastal waters, but there are no actual data to confirm this. Further, because there has been little offshore phytoplankton sampling, it is not possible to determine whether blooms originate at one or several sites or whether isolated blooms develop simultaneously in several locations in response to similar hydrographic conditions (Price et al. 1991). It is also difficult to establish whether blooms develop offshore before they are detected in coastal waters (usually evident only from increasing toxicity in the mussels used for monitoring).

In Puget Sound, a fjord with a long, deep, main channel and numerous relatively shallow, often poorly flushed bays on the western and southern margins, blooms are probably not linked to those along the open coast, but instead originate in situ. Toxicity may be widespread or highly localized (Nishitani and Chew 1988). In some areas, the onset of early summer blooms of *A. catenella* and the resultant mussel toxicity is dependent on development of a warm (14°C) surface layer several meters thick (Nishitani and Chew 1984). Other factors that may control the onset and duration of blooms in inland waters are nutrients (N and P), reduced turbulence, and parasitism by the dinoflagellate *Amoebophyra ceratii* (Taylor 1968; Nishitani et al. 1984, 1985; Nishitani and Chew 1984).

A combination of physical and nutrient-supply factors may explain why PSP has not been a problem in Hood Canal, another western Washington fjord (Rensel 1993*a*). Sustained estuarine outflow coupled with strong mixing at the mouth may prevent cells from entering, and nitrogen levels in central Hood Canal may be too low to support blooms elsewhere in the canal. However, there have been blooms of *Alexandrium* in Quilcene Bay–a small, relatively shallow arm of Hood Canal (C. Edwards pers. comm.; R Horner unpubl. obs.).

Domoic acid poisoning (DAP)—Domoic acid poisoning first became a concern on the U.S. west coast in September 1991 when more than 100 brown pelicans and cormorants in Monterey Bay died or suffered from unusual neurological symptoms (Fritz et al. 1992; Work et al. 1993). This event was eventually linked to the neurotoxin domoic acid, and the source was identified as a bloom of the diatom *Pseudo-nitzschia australis* (Buck et al. 1992; Fritz et al. 1992; Garrison et al. 1992).

By late October and November 1991, domoic acid was found in razor clams (*Siliqua patula* Dixon) and Dungeness crabs (*Cancer magister* Dana) on the Oregon and Washington coasts. A few people became ill in Washington after eating razor clams, but their symptoms were mild and short lived, and health officials were not able to confirm whether the illnesses were caused by domoic acid. No specific source organism is known for the Oregon-Washington event, but Taylor and Horner (1994) suggested that it might have been part of a widespread bloom of *P. australis.* Such a bloom, starting in California in September, and carried up the coast by the Davidson Current at a speed of nearly 20–40 cm s^{-1}, could have reached the Washington coast by late October–November—the time when razor clams were found to be toxic (C. Ebbesmeyer pers. comm.; B. Hickey pers. comm.).

Since the seabird deaths in 1991 and until about 1994, domoic acid and *Pseudo-nitzschia* species were monitored in the shallow waters of Monterey Bay (Buck et al. 1992; Walz et al. 1994). At the peak of the 1991 toxic event, domoic acid levels in coastal waters reached >10 μg $liter^{-1}$ and abundances of *P. australis* were $>10^6$ $liter^{-1}$ (Walz et al. 1994). Since then, domoic acid has been detected in both autumn and spring plankton assemblages, but with concentrations usually <1 μg and cell densities 1–2 orders of magnitude lower than in 1991. Blooms during the 1991–1994 period often have been comprised of two or three potentially toxic species (i.e., *P. australis, Pseudo-nitzschia multiseries,* and *Pseudo-nitzschia pseudodelicatissima*). Based on cell volume dominance, however, most of the domoic acid measured in plankton assemblages must have been contributed by *P. australis* (Walz et al. 1994, unpubl. data).

During the 1991–1994 period, blooms of *P. australis* were most common and persisted longer during late summer and autumn when hydrographic conditions are associated with the end of the upwelling season (Bolin and Abbott 1963; Garrison 1979) and are usually characterized by warmer sea-surface temperatures, thermal stratification, and lower concentrations of inorganic nutrients (Buck et al. 1992; Walz et al. 1994). Blooms also occurred during spring upwelling, but were less well developed and generally shorter in duration (Walz et al. 1994).

The relationship between production of domoic acid by *Pseudo-nitzschia* spp. and environmental conditions is not clear. In batch culture, domoic acid production by *P. multiseries* is restricted to the stationary growth phase in silicate-limited culture conditions (Subba Rao et al. 1988; Bates et al. 1989, 1991). Garrison et al. (1992) speculated that if toxin production dynamics are similar for *P. australis,* then toxic events may be limited to seasons when stratification and nutrient depletion occur or to nearshore regions where developing blooms deplete the dissolved nutrients. However, field observations in Monterey Bay (Walz et al. 1994) show that domoic acid is produced in *P. australis* at low cell densities and at moderate nutrient concentrations, suggesting a pattern different from that of *P. multiseries.* Alternatively, results from batch culture experiments cannot be extrapolated to natural populations.

The domoic acid poisoning in Monterey Bay in 1991 was unusual because the vector was northern anchovies, not shellfish (Work et al. 1993). The highest concentrations of domoic acid, up to 2,300 $\mu g\ g^{-1}$ wet weight of tissue, were found in the viscera of anchovies (Loscutoff 1992), apparently in the form of undigested *P. australis* cells. Anchovies in the central California region are eaten by marine mammals, several finfish (Morejohn et al. 1978), and occasionally humans. Domoic acid has been found also in some grazing zooplankton (Buck et al. 1992; Haywood and Silver unpubl.). With the exception of seabirds, there is no evidence of effects or impacts of domoic acid on the pelagic food web. Further, when fish meal made from toxic anchovies collected in Monterey Bay during the 1991 outbreak was fed to juvenile rainbow trout (*Oncorhynchus mykiss* Walbaum), domoic acid was found only in the viscera and feces, not in blood or muscle. This suggests that domoic acid in fish food probably does not constitute a health hazard either to the fish or to the consumer (Hardy et al. 1995). There is speculation that domoic acid may have been associated with historical autumn seabird mortalities (Buck et al. 1992). In August 1961, for example, a large flock of sooty shearwaters that had fed on anchovies in Monterey Bay invaded one of the coastal cities and exhibited unusual behavior suggestive of domoic acid intoxication (Garrison and Walz unpubl.; Mestel 1995).

The source of domoic acid in razor clams and Dungeness crabs in the Pacific Northwest has not been determined. No phytoplankton samples are available from offshore, and samples collected from ocean beaches usually contain few cells of *Pseudo-nitzschia* spp. (Jijina and Lewin 1983; Horner and Postel 1993; R. Horner unpubl. obs.). However, most fall and spring recreational harvests of razor clams have been affected by the continued or new presence of domoic acid in the clams. Not all harvest areas are affected and not all clams on one beach contain similar amounts of domoic acid (J. Wekell pers. comm.). Depuration of domoic acid by razor clams apparently is a long-term process (Drum et al. 1993; Horner et al. 1993).

Willapa Bay and Grays Harbor on the Washington coast are sites of intense oyster culture, but domoic acid has not been found in the oysters. Reasons for this are unclear because *Pseudo-nitzschia* spp., including *P. australis* and *P. multiseries,* are found in Willapa Bay, but only when the salinity is near 28–29 psu (Sayce and Horner 1996), indicative of the intrusion of high-salinity ocean water. When *Pseudo-nitzschia* spp. occur in the bay, they remain for several months (Sayce and Horner 1996).

Elsewhere in western Washington, blooms of *Pseudo-nitzschia* spp. usually have been short lived, and shellfish are rarely toxic. However, in fall 1994, a bloom of *Pseudo-nitzschia pungens, P. multiseries,* and *P. australis* persisted in Hood Canal for >6 weeks. Mussels, the sentinel organism used by the Washington Department of Health to test for algal toxins, contained ~10 $\mu g\ g^{-1}$ wet weight of domoic acid and the phytoplankton ~14 $\mu g\ g^{-1}$ wet weight. This was the first time since domoic acid monitoring began in 1991 that relatively high levels were found in mussels and in inland waters of western Washington (Horner et al. 1996). However, the use of mussels as the sentinel species may not be appropriate for domoic acid testing because they are reported to take up the toxin rapidly but also to depurate rapidly, whereas other bivalves retain domoic acid for longer periods (Novaczek et al. 1991; Drum et al. 1993; Horner et al. 1993). The *Pseudo-nitzschia* bloom has not recurred in Hood Canal (R. Horner unpubl. obs.).

Alaska does not have a severe problem with domoic acid, although potentially toxic *Pseudo-nitzschia* spp. have been identified in Alaskan waters (R. Horner unpubl. obs.; R. RaLonde unpubl. obs.; L. Smith unpubl. obs.). Approximately 3,000 samples, primarily commercially valuable shellfish and finfish, have been tested since 1992. The highest domoic acid value was 11.1 $\mu g\ g^{-1}$ (for a razor clam) with only 17 values of 2 $\mu g\ g^{-1}$ or greater being reported (R. Barrett pers. comm.).

Domoic acid production has been confirmed for five species of *Pseudo-nitzschia* (Table 1). All have been reported from the west coast, and toxin production by locally isolated clones has been confirmed for *P. australis* (Garrison et al. 1992), *P. multiseries* (Villac et al. 1993*a*), and *P. pungens* (Trainer et al. in prep.). The distribution of potentially toxic *Pseudo-nitzschia* species along the Pacific coast is not clear because *Pseudo-nitzschia* has often been identified only to the genus level and nontoxic forms exist. The record of *P. australis* in particular, is confusing because early reliable records suggested it was confined to the southern hemisphere (Hasle 1972). However, Garrison re-examined samples from a massive *Pseudo-nitzschia* bloom in Monterey Bay in December 1977, and confirmed the presence of *P. australis* in California at least 14 yr before the first report of toxicity. He speculated that *P. australis* may have been regularly misidentified as the morphologically similar *Pseudo-nitzschia seriata* (Garrison et al. 1992; *see also* Villac et al. 1993*a,b*). If so, then *P. australis* (and thus DAP) may have a long history on the Pacific coast (e.g. Gran and Thompson 1930; Cupp 1937; W. E. Allen's data as summarized by Lange et al. 1994; Garrison 1979; Schrader 1981; Smith 1991).

Fish kills—The diatoms *C. convolutus* and *C. concavicornis* have caused the death of finfish reared in net pens since at least 1961 (Bell 1961); *C. danicus* has also been implicated. Early reports (Bell 1961) suggested that setae were likely to break off the diatom cells, penetrate the fish gills, and be trapped by small spines on the setae. Fish death was attributed to suffocation from excessive mucus production by the gills, bacterial infections resulting from the injury, or bleeding from the gills. Recent investigations have found little evidence that diatom setae actually penetrate the gill tissue. Instead, the primary mechanism seems to be reduction of gas exchange in the gills caused by mucus production when the gill epithelium is irritated by *Chaetoceros* setae wedged between the secondary lamellae (Rensel 1993*b*). These *Chaetoceros* spp. are frequently present, albeit in low numbers in the phytoplankton community in the Pacific Northwest and usually do not form blooms, although on occasion *C. concavicornis* may be abundant (e.g. Dabob Bay in October 1991 at 10^5 cells liter^{-1} J. Postel unpubl. obs.). These *Chaetoceros* species are also found in California and Alaska waters, but do not have a negative impact because there is little finfish farming (it is illegal in Alaska).

However, *C. convolutus* has been implicated in the mortality of juvenile red king crabs [*Paralithodes camtschatica* (Tilesius)] at Unalaska Island. Cells and setae were the dominant component of the debris in the mucous covering of the damaged crab gills (Tester and Mahoney 1995).

Pen-reared salmon mortality has also been associated with the raphidophyte flagellate *H. akashiwo* since 1976. There have been blooms of *Heterosigma* in British Columbia waters every year since the 1960s; fish kills have been reported most years since 1986 in British Columbia and in some years (1989, 1990) in Washington. Resultant losses to the fish growers are about \$4–5 million per year (Taylor and Horner 1994). Wild salmon died during a *Heterosigma* bloom in fall 1994 in the northernmost part of Case Inlet off southern Puget Sound. What actually causes the fish deaths is presently unknown, although *Heterosigma* is reported to produce superoxide and hydroxyl radicals and hydrogen peroxide (Yang et al. 1995) and an ichthyotoxin (R. A. Cattolico pers. comm.).

The cause(s) of *Heterosigma* blooms are also unclear, but populations in the Strait of Georgia and northern Puget Sound may be enhanced due to agricultural runoff from the Fraser River; however, *Heterosigma* also has bloomed on the outer coast of Vancouver Island where there is little agricultural runoff (Taylor and Horner 1994). In British Columbia, *Heterosigma* usually does not bloom until the water temperature reaches 15°C and the salinity is reduced to ~15 psu by runoff from the Fraser River (Taylor and Haigh 1993). In central Puget Sound, *Heterosigma* blooms apparently originate in shallow back bays and are carried into deeper water by tidal currents. There is some indication from laboratory experiments that *Heterosigma* responds to salinity gradients, migrating to the surface of test tubes upon addition of a thin layer of freshwater (Hershberger 1995). Moreover, cells remained above the halocline, possibly by changing their density. Thus a bloom may require heavy rainfall or runoff followed by mild weather with little wind which allows the water column to stratify long enough for cells to accumulate at the surface (Hershberger 1995).

Red tides—Visible red tides are common on the central and southern California coasts, but there has been no concentrated effort to characterize their seasonal or spatial occurrences. There were only four conspicuous red tides in a 20-yr record from ~1920 to 1940 (Allen 1941). However, there were red tides in southern California in 10 of the years between 1952 and 1974; thus they may be an annual, but often unreported occurrence (Sweeney 1975). Other red tides have been observed by members of the Food Chain Research Group at Scripps Institution of Oceanography in coastal waters off La Jolla from 1967 to 1974. Causative taxa include *Lingulodinium polyedrum, Prorocentrum micans, Gymnodinium sanguineum, Gymnodinium flavum, Ceratium furca, Ceratium fusus, Ceratium* spp., *Protoperidinium* spp., and the ciliate, *Mesodinium rubrum.* From 1963 to 1980 in central California, *Protoperidinium* spp., *Ceratium* spp. (especially *C. dens* and *C. furca*), *L. polyedrum,* and *P. micans* have formed red tides (Abbott and Albee 1967; D. Garrison unpubl. obs.). They are most common during mid- to late summer when coastal upwelling is sporadic or has ceased and stratified conditions prevail. However, a bloom of *L. polyedrum* extended from Santa Barbara to south of the Mexican border in January 1995, possibly the result of unusually heavy rains that brought extensive nutrient-rich runoff into the coastal region. A few weeks later, there was an extensive *Noctiluca* bloom in the same area (Howard 1996). None of these red tides have been associated with toxin production or fish kills. However, dense blooms of red tide organisms are known to reduce grazing rates of some zooplankton (e.g. Fiedler 1982; Huntley 1982), but some species appear to be beneficial as food for larval fish (e.g. Hunter and Thomas 1974; Scura and Jerde 1977; Lasker and Zweifel 1978). As a result, it is difficult to assess the overall effect of these events on pelagic food webs.

Less is known about nontoxic red tides elsewhere along the coast. Blooms of the dinoflagellates *C. fusus* and *G. sanguineum* often occur in late summer and fall in shallow, back-bay areas in southern Puget Sound. Mortalities of oyster larvae and adults [*Crassostrea gigas* (Thunberg)] and spot prawns (*Pandalus platyceros* Brandt) have been associated with these blooms (Cardwell et al. 1977, 1979; Rensel and Prentice 1980), but there is no indication of a chemical toxin and death may be due to mechanical damage or oxygen stress created when the blooms decay.

There were massive blooms of *C. furca, Ceratium divaricatum,* and *P. micans,* lasting 1–3 months between August and November, off the Washington coast in 1994 and 1995. There were apparently no shellfish or other mortalities, but razor clams on coastal beaches and oysters in Willapa Bay and Grays Harbor turned pink. The color in the razor clams was in the meat, while in the oysters, it remained in the viscera and turned the canning liquid pink after a few days, causing economic losses for shellfish growers who could not sell their tainted product.

In Alaska, nearshore waters are nutrient enriched in spite of the strong prevailing winds which result in a downwelling-dominated system during most of the year. Occasionally, and under conditions that are not well understood, blooms of *Phaeocystis* sp. occur, either as a major component of the spring bloom or as a later, secondary bloom. *Phaeocystis* has been implicated in the production of both acrylic acid and β-dimethylsulfoniopropionate (DMSP) (Barnard et al. 1984; Slezak et al. 1994). Some evidence indicates that this alga is not readily eaten by invertebrates in the water column, but it is not certain whether zooplankton are unable to graze *Phaeocystis* because it forms large colonies, because it accumulates these chemicals, or both (Estep et al. 1990). Actively growing cells are apparently avoided by grazers, but once growth slows, *Phaeocystis* can become a preferred food item (Estep et al. 1990), thus altering grazing patterns and therefore carbon and energy flow through the ecosystem. Perhaps the intermittent *Phaeocystis* blooms can be linked to physical forcing factors pertaining to the mixing of nutrient-rich deep waters into the euphotic zone. Seabird deaths were reported near a *Phaeocystis* bloom in Dutch Harbor, Alaska, in September 1991, but a possible relationship was not apparent (D. Knox pers. comm.).

A serious problem in Alaska is bitter crab disease, which affects the valuable Tanner crab fishery (annual ex-vessel value ~\$2.3 million). The cause is a *Hematodinium*-like, parasitic dinoflagellate that affects crabs during their summer molt (Meyers et al. 1987; Love et al. 1993). The parasite multiplies quickly and reaches high densities in the hemolymph and internal organs and is 100% fatal. Its life cycle has not been characterized. This is not a typical planktonic bloom organism, but we mention it here because of its effects on a valuable commercial fishery and the possibility that it may spread to other crab species and(or) other geographical areas. More importantly, crabs are frequently the dominant prey in the diets of at least seven species of invertebrates, 26 species of fish, and four species of marine mammals (Jewett 1982). An estimated 1.5×10^{10} crabs are eaten annually by Pacific cod in the Kodiak area alone. Demise of this large Tanner crab population would obviously have a significant impact on its prey populations, mostly juvenile Tanner crab (*Chionoecetes bairdi* Rathbun), other arthropods, fishes, and molluscs (Jewett and Feder 1983).

Discussion

The threat of harmful algal blooms and their consequences exist all along the west coast of North America. This is a vast area covering nearly 30 degrees of latitude (~60°N in the Gulf of Alaska to ~30°N in southern California), but with much more coastline because of fjords, inlets, islands, bays, and estuarine areas. Outbreaks continue at unexpected times and in unexpected places (e.g. the domoic acid event in 1991). Generally, the same harmful phytoplankton species are found throughout the region despite the diverse hydrographic conditions. Most of the fjords, estuaries, and enclosed embayments are north of the Columbia River, long, straight stretches of coastline with sandy beaches are found in Oregon and Washington, and rocky shores are more common in California and Alaska. The amount of freshwater in the form of precipitation and runoff also varies, with highest amounts in the north. Thus, although the Pacific states have similar harmful species, the environmental features affecting blooms may be similar or quite different.

Most of the socio-economic and ecological issues associated with HABs are apparent along the west coast. Within the region, blooms of toxic and nontoxic species extend over wide geographic areas. Fish kills, some caused by species (e.g. *Heterosigma*) that do not become noticeable until fish die (the so-called hidden flora), are regular occurrences in the Pacific Northwest. Consequently, extensive monitoring programs are in place to detect their presence at low concentrations. There is evidence of food-web interactions (e.g. DAP, anchovies, and birds) and the potential for introduction of toxic organisms from other geographic areas, as well as range extensions of indigenous taxa via human activities (e.g. ballast water transport) or natural phenomena (e.g. current transport). Further, there is a great disparity in the amount of information about HABs available over the area. We have not specifically included British Columbia in our discussion, but the same problems exist there as elsewhere along the Pacific coast (e.g. Prakash and Taylor 1966; Chiang 1985; Gaines and Taylor 1985; Forbes and Denman 1991; Haigh and Taylor 1990; Taylor et al. 1994; Taylor and Horner 1994).

It is evident from early records (e.g. Meyer et al. 1928; Quayle 1969), local native customs (e.g. Meyer et al. 1928; Cameron 1981), and the apparent ability of some native marine animals to distinguish toxic prey species (Kvitek 1993) that PSP has been present on the west coast for hundreds of years, perhaps longer (Taylor and Horner 1994). Unfortunately, there are few historical records of toxic phytoplankton species except in California where samples have been collected from the Scripps Institution of Oceanography pier since the 1920s (e.g. Allen 1928; Lange et al. 1994) and in Monterey Bay (e.g. Bolin and Abbott 1963; Garrison et al. 1992; Buck et al. 1992; Walz et al. 1994). In Washington, there are a few records from the 1920s and 1930s from the San Juan Islands (Johnson 1932; Phifer 1933) and later from the Strait of Juan de Fuca (Chester et al. 1979). Jijina and Lewin (1983) collected extensively in the surf zone between southern Oregon and central Washington but did not report any toxic species.

Historical records from Alaska are even more sparse. A *Gonyaulax* sp. (possibly *Alexandrium* using modern terminology) was reported from Jack Bay (Prince William Sound) (Alexander and Nauman 1969), Tenakee Harbor (Zimmerman and McMahon 1976), some southeast Alaska sites (Chang 1971), and near Ketchikan (Sparks 1966; Neal 1967). Cupp (1943) reported large numbers of *Nitzschia seriata* at Scotch Cap, and *Nitzschia pungens* and *N. seriata* were found sporadically in the Port Valdez area during cruises from May 1971 to April 1972 (Horner et al. 1973). Identifications of the *Nitzschia* species were made only with the light microscope however, and may be in correct.

The physical and chemical characteristics of coastal waters along the North American west coast are determined primarily by large-scale climatic events (e.g. Reid et al. 1958). Latitudinal gradients in climate, variations in topography, and differing mesoscale circulation dynamics result in several distinct regional habitats (U.S. GLOBEC 1994). However, hydrographic mechanisms underlying the HAB problem along the west coast are poorly understood. There have been no sustained field programs combining physical oceanography and HABs, so bloom dynamics and physical forcings remain significant and important unknowns. For PSP, a good case can be made that northern California outbreaks follow the relaxation of seasonal upwelling. A retrospective study of meteorological data, shellfish toxicity records, and remote-sensing images of sea surface temperature indicate that many PSP outbreaks near Drakes Bay (Marin County) occur when winds shift in the late summer and cause upwelling to relax. This forces warm, offshore waters and their associated *Alexandrium* populations onshore, resulting in rapid increases in PSP toxicity (D. M. Anderson unpubl. data). A resumption of upwelling winds replaces the warm nearshore waters with deep, cold water containing no *Alexandrium* cells, and toxicity in shellfish begins to decrease. This scenario, although appealing and consistent with several independent datasets, presumes an established, offshore population of *Alexandrium,* which until now has not been reported, perhaps due to the lack of appropriate sampling programs at the right places and times. This raises the interesting questions of how extensive the putative offshore population of toxic *Alexandrium* is along the U.S. west coast and what the hydrographic features are that maintain bloom populations before their delivery to nearshore waters. A similar mechanism linking shellfish toxicity to changes in upwelling conditions has been reported for rias along the northwest coast of Spain where hydrographic conditions resemble those along the California coast (Fraga et al. 1988). Offshore blooms of *Gymnodinium catenatum* were hypothesized and eventually documented.

Some, but not all, HAB outbreaks on the Pacific coast coincide with ENSO events (Erickson and Nishitani 1985; Garrison unpubl. obs.). For example, the 1991 domoic acid event may have been associated with unusually warm weather and northward movement of warm waters caused by El Niño. However, in Oregon and Washington, the incident followed rain after a 45-d dry period—the same conditions found in eastern Canada during the first outbreak in 1987 (Bird and Wright 1989; Horner and Postel 1993). This suggests that stratification and stability are necessary for bloom development.

Dispersal mechanisms for potentially harmful species are not known for the Pacific coast. *Alexandrium* spp. produce resting cysts (hypnozygotes) that may be transported by currents, storms, or other natural phenomena in the same manner as sediment particles, settling to the bottom in new locations and remaining dormant until conditions are right for germination. Moreover, the cysts also may be transported to new locations in ballast water, but species introductions have not yet been documented for the Pacific coast. *Pseudo-nitzschia* spp. are not known to produce cysts or resting spores, so their manner of dispersal is probably by currents and other natural means. Because the vegetative cells are photosynthetic, they may not survive long, dark periods in ballast tanks.

There is some evidence that PSP in Washington has spread southward into Puget Sound since 1978 following a widespread outbreak in Whidbey basin (northern Puget Sound), which may be related to some single-step climatic event that happened in the Pacific Northwest in 1976 (Ebbesmeyer et al. 1991). More recently, decadal variation of PSP in Sequim Bay, on the Strait of Juan de Fuca, was compared with selected environmental factors (Ebbesmeyer et al. 1995). Results suggest that when the climate is warm and dry, PSP toxicity increases, whereas during cold, wet years, PSP toxicity decreases. Further, average toxin concentrations in June through August increased ~3-fold between 1964–1975 and 1980–1991. If the predicted environmental cycles persist, then it is reasonable to assume that the current warm, dry regime in the Pacific Northwest will soon revert to a cold, wet regime and PSP outbreaks will decrease (Ebbesmeyer et al. 1995).

Although vast areas of the coast are affected by PSP and(or) DAP, the source of the causative populations and the hydrographic and environmental factors that contribute to the blooms generally are not known. For example, was the large-scale domoic acid event in 1991 caused by a single bloom extending from California to British Columbia or were there multiple blooms all caused by similar hydrographic conditions? Moreover, it has been shown that potential domoic acid producers have been present in southern California since the 1930s (Lange et al. 1994) and in Monterey Bay at least since the 1970s (Garrison 1979). A similar species, *P. seriata,* now known to be a domoic acid producer (Lundholm et al. 1994), has been reported in Washington waters since the 1930s (Johnson 1932; Phifer 1933), and domoic acid was found in razor clams harvested between 1985 and 1991 (Natl. Mar. Fish. Serv. unpubl. data). Domoic acid was also found in a number of benthic crustaceans (Loscutoff 1992; Langlois et al. unpubl.), but the sources and pathways transferring domoic acid to the benthic community have not been established and there have been no studies to determine how accumulated toxin may affect secondary consumers. The unusual, but similar, behavior of seabirds in Monterey Bay in 1961 and 1991 suggests that domoic acid has been present on the west coast for many years, but just not recognized. If so, the effects on the human population have been mild.

The need for routine phytoplankton monitoring often has been stressed (e.g. Gaines and Taylor 1985; Taylor and Horner 1994), but it has not been effectively implemented except in a few areas (e.g. Monterey Bay, some fish farms in western Washington). Phytoplankton monitoring programs by state health departments in California and Washington and by the Alaska Sea Grant Program in the last few years, however, have provided some much needed information on the spatial and temporal distributions of potentially toxic species. Meanwhile, both aquaculture and the harvest of wild shellfish continue to grow in all the west coast states. The harvest of nontraditional shellfish, such as moonsnails, whelks, and barnacles, is increasing and will lead to new human health problems and the need for increased management of these resources (Matter 1993; Shumway 1995).

This brief discussion leaves us with more questions than answers: What is the source of the populations for both ocean coast and estuarine blooms of all the major HAB species? What hydrographic and environmental factors contribute to blooms? Can outbreaks be tied to the transport of offshore waters, and, if so, can this transport be detected and possibly predicted by remote sensing? How extensive are blooms, including nontoxic red tides? What are the seasonal and geographic distributions of the HAB species? What are the life cycles of the west coast HAB species? Do life cycles, especially the presence of resistant spores and cysts, influence the distribution and population cycles of HAB species? Can an understanding of bloom dynamics be used to guide the development of the shellfish industry? How effective are phytoplankton monitoring programs for understanding bloom dynamics? What are the effects of HABs on local food webs and west coast ecosystems in general? These questions are generic and could be asked for nearly all coastal areas where HABs occur. Future research projects on the U.S. west coast should address these questions because outbreaks of toxic algae will continue and likely will increase, new toxins will be found, more species will be found to produce toxins, and more fisheries resources will be affected.

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